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Systematics of *Stenocercus chrysopygus* Boulenger, 1900 (Squamata, Tropiduridae) species complex using genetic and morphological evidence

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Abstract

The assessment of the taxonomic status of *Stenocercus chrysopygus* Boulenger, 1900, a conspicuous species inhabiting the upper valleys of the Santa, Chiquián, and Marañón rivers in central Peru, has been pending for decades. We studied the phylogenetic relationships and variation of several populations using mitogenomes, DNA barcode datasets, and morphological evidence. We present a phylogeny of *Stenocercus* combining available mitochondrial sequences with 37 mitochondrial genes from *S. chrysopygus* and closely related congeners samples. Our results support *S. chrysopygus* as a species complex, with three additional species among the studied populations. Populations from the Santa River valley, including all syntype localities, correspond to *S. chrysopygus* sensu stricto.

Key Words

Andes, mitogenome, morphology, species delimitation, phylogeny, tropidurid lizards

Introduction

The highest diversity of *Stenocercus*, a widespread genus in South America, occurs in the Andes (Torres-Carvajal 2007a; Torres-Carvajal and Mafla-Endara 2013). Notably, the Peruvian Andes concentrate 65% of the 80 currently known species of *Stenocercus*; among them, 42 are endemic, and 19 were described in the last 20 years (Uetz et al. 2025). This high species description rate is mainly due to the discovery of new species in unexplored areas (Venegas et al. 2014, 2016, 2020a, 2020b, 2022; Köhler and Lehr 2015; Mendoza et al. 2021). However, the herpetological fauna of the Peruvian Andes remains poorly explored, so new species await discovery both in the field and among museum specimens. For instance, the taxonomic status of the populations of *S. chrysopygus* Boulenger, 1900, an endemic species described more than a century ago, has remained unresolved. This species is currently known from the upper valleys of the Santa, Chiquián, and Marañón rivers, at elevations between 2265 and 3500 m, in Áncash and Huánuco departments in central Peru (Fritts 1974; Cadle 1998; Torres-Carvajal 2007a), with scattered populations on the eastern and western slopes of the Cordillera Occidental and on the eastern slope of the Cordillera Oriental (Fritts 1974; Cadle 1998; Torres-Carvajal 2007a). Conspicuous variation in color among adult males from geographically isolated populations has been reported (Fritts 1974; Cadle 1998; Schlüter 1999, 2000, 2001, 2005; Torres-Carvajal 2007a). For instance, the coloration on the ventral thighs and pelvic region of males from syntype localities in the Santa River valley is dull yellow, whereas males from the Chiquián and Marañón

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river valley localities have black coloration (Fritts 1974). Additionally, individuals from the Marañón River valley have higher counts of vertebral scales and scales around midbody (Fritts 1974; Cadle 1998).

We conducted an integrative study combining morphological data from museum specimens and new material from an expedition directed to sample populations across the *Stenocercus chrysopygus* distribution and molecular data from complete mitochondrial genome sequencing of all sampled populations. We present a new phylogeny of *Stenocercus* and demonstrate the existence of three additional species among *S. chrysopygus* studied populations.

Methods

Fieldwork

We conducted an expedition to collect *Stenocercus chrysopygus* specimens from both the eastern and western slopes of the Cordillera Negra and Cordillera Blanca, including syntype localities. We also collected specimens of *S. amydrorhytus* Köhler & Lehr, 2015, and *S. johaberfellneri* Köhler & Lehr, 2015, two species endemic to the Áncash department, from type localities. Specimens were collected by hand or using a noose, photographed, euthanized, fixed in formalin for 24 hours, and transferred to 70% ethanol for storage. Before the formalin treatment, a tissue sample (muscle and/or liver) was extracted and preserved in 96% ethanol. All specimens and tissue samples are deposited in the Herpetology Department at the Museo de Historia Natural de San Marcos (MUSM) (Suppl. material 1).

DNA extraction and sequencing

We extracted DNA from muscular and hepatic tissue from specimens collected during fieldwork and from tissues stored in the MUSM collection from *Stenocercus amydrorhytus*, *S. chrysopygus*, *S. cupreus* Boulenger, 1885, *S. johaberfellneri*, *S. latebrosus* Cadle, 1998, *S. melanopygus* Boulenger, 1900, and *Microlophus thoracicus* (Tschudi, 1845). A Zymo Research Quick-DNA Miniprep Plus Kit, with 4 µL of RNase A solution (4 mg/ml; PROMEGA) added to the first step, was used for DNA extractions. Genomic DNA was delivered to CD Genomics (NY, USA) for genomic library construction and sequencing using the Illumina PE150 platform.

Bioinformatic analyses

Quality filtering analyses and mitogenome assembly were run on the Facultad de Ciencias Biológicas UNMSM server. Raw reads were filtered and adaptors removed using FASTP 0.20.0 (Chen et al. 2018). The quality of filtered sequence data was assessed with FASTQC 0.11.3 (Andrews 2010). Mitogenomes were assembled using GETORGANELLE 1.7.5+ (Jin et al. 2020). When GETORGANELLE output multiple FASTA files, the first one was selected for downstream analyses. If GETORGANELLE produced scaffolds, the longest was selected. Assembled mitogenomes were visualized using BANDAGE 0.8.1 (Wick et al. 2015). Gene annotation was conducted using the online MITOS2 tool (Al Arab et al. 2017; Donath et al. 2019) on the Galaxy platform. If duplicated genes were reported, mitogenomes were visualized in GENEIOUS Prime 2025.0.3 to check position and composition. Only correctly positioned genes were used in subsequent analyses; shorter and mispositioned duplicates were discarded. The circular mitogenome map of *Stenocercus chrysopygus* was drawn using GENEIOUS Prime.

Phylogenetic analyses

We built the DNA sequence matrix with new sequences and 416 sequences downloaded from GenBank, representing 15 mitochondrial regions from 41 *Stenocercus* terminals (Suppl. material 2). Available sequences in GenBank correspond to the following mitochondrial genes: NADH dehydrogenase subunit 1 (ND1), tRNA-Ile, tRNA-Gln, tRNA-Met, NADH dehydrogenase subunit 2 (ND2), tRNA-Trp, tRNA-Ala, tRNA-Asn, tRNA-Cys, tRNA-Tyr, tRNA-Val, cytochrome oxidase I (COI), cytochrome b (cytb), 16S rRNA, and 12S rRNA. We also included a 574 bp ND2 sequence of *Stenocercus modestus* (PX102407) provided by M. Vences. *Microlophus thoracicus* was used to root all trees.

All mitochondrial genes were aligned online using MAFFT 7 (Kuraku et al. 2013; Katoh et al. 2019). The G-INS-i strategy was used to align protein-coding genes (PCGs), and the Q-INS-i strategy for tRNA and rRNA. Sequences from COI, cytb, and ND1 were aligned in two non-overlapping groups. Alignments were visualized in ALIVIEW 1.28 (Larsson 2014). Stop codons at the end of PCG alignments were removed. All aligned matrices were concatenated in SEQUENCE MATRIX 1.7.8 (Vaidya et al. 2011). A partition analysis was performed using MODELFINDER, with the options TESTNEWMERGEONLY and -rcluster 50 selected (Kalyaanamoorthy et al. 2017). Model selection under BIC and tree searches was simultaneously performed (Chernomor et al. 2016; Kalyaanamoorthy et al. 2017). Phylogenetic analyses were performed using the IQ-TREE web server (Trifinopoulos et al. 2016) under the maximum-likelihood (ML) criterion. IQ-TREE search parameters were left at default values. We ran 50 independent tree searches. Branch support was assessed through 1000 ultrafast bootstrap (UB) replicates (Hoang et al. 2018) and SH-aLRT branch tests. We considered values of UB and SH-aLRT to be high when ≥ 95 and 80, respectively (Guindon et al. 2010; Minh et al. 2013).

Genetic distances

Uncorrected p-distances were calculated using MEGA 11.0.13 (Tamura et al. 2021) for cytb (1,137 bp) and COI (1,545 bp) (Frost et al. 1998; Carvalho et al. 2018) among *Stenocercus chrysopygus* and *S. johaberfellneri* samples.

Species delimitation analyses

We performed species delimitation using two methods: Assemble Species by Automatic Partitioning (ASAP) (Puillandre et al. 2021) and Bayesian implementation of the Poisson Tree Processes (bPTP) (Zhang et al. 2013). ASAP was run on ASAP web (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html) using Simple Distance (p-distances) on COI and cytb aligned sequences. For the bPTP analysis, a single run of tree search was conducted in IQ-Tree using a matrix of COI and cytb sequences. The tree-based bPTP method was run on the online server (https://species.h-its.org/ptp/) on the rooted tree with 500000 MCMC generations.

We calculated the Relative Taxonomic Resolving Power Index (Rtax) and the Taxonomic Index of Congruence (Ctax), proposed by Miralles and Vences (2013), to compare the results of the species delimitation methods. The Rtax quantifies the ability of a method to reveal a high number of potential candidate species, relative to other methods. A method with high Rtax indicates high relative resolving power, minimization of beta-error (false negatives), but possible maximization of alpha-error (false positives). The Ctax compares congruence of taxonomies inferred by two methods. A high Ctax indicates that both methods inferred the same potential candidate species, whereas a low Ctax indicates underestimation, overestimation, or misestimation by at least one of the methods.

Morphological data and analyses

We examined 240 adult specimens of *Stenocercus chrysopygus* (Suppl. material 1). Sex of adults – specimens with SVL larger than 46 mm – was determined by noting the presence of hemipenes and color pattern. Of these, 173 had complete data for all selected characters and were included in morphological analyses. We also included data from five *S. johaberfellneri* adult specimens (Suppl. material 1). The following six characters were measured: snout–vent length (SVL), head width (HW), head height (HH), head length (HL), humerus length (HmL), and femur length (FL). Before analyzing morphometric data, we analyzed male and female data in a PCA in PAST 4.03 (Hammer et al. 2001) to evaluate if data were grouped by sex.

The following scale counts were taken, as described in Torres-Carvajal (2000): gulars (GS), scales around midbody (SM), vertebrals (VS), and paravertebrals (PS). Measurements were taken with a manual caliper to the nearest 0.05 mm.

Fold definitions follow Torres-Carvajal (2000). Life coloration of *Stenocercus chrysopygus* was observed from live photographs, and for *S. johaberfellneri*, from both live photographs and the original description (Köhler and Lehr 2015).

Multivariate analysis

Six morphometric and four meristic characters were evaluated using Discriminant Function Analysis (DFA) in PAST 4.03. Groups were defined following results from the phylogenetic analysis.

Gaps in morphology

We inferred gaps in morphology, following the method of Zapata and Jiménez (2012), for six morphometric and four meristic characters. The frequency cutoff for analyses was 0.1 (Zapata and Jiménez 2012). Analyses were run in RSTUDIO (Posit team 2024) using the packages labdsv (Roberts 2023), ellipse (Murdoch and Chow 2023), mvtnorm (Genz and Bretz 2009), vegan (Oksanen et al. 2025), and spdep (Bivand and Wong 2018). Groups were defined following results from the phylogenetic analysis.

Results

Mitogenomes

We obtained 47 *Stenocercus* mitogenomes: *Stenocercus chrysopygus* 15,584–19,673 bp, *S. amydrorhytus* 17,320–17,482 bp, *S. cupreus* 17,123 bp, *S. johaberfellneri* 17,156–18,803 bp, *S. latebrosus* 17,332 bp, and *S. melanopygus* 15,663–17,489 bp. We also obtained two *Microlophus thoracicus* mitogenomes (17,613–17,865 bp). Sequenced mitogenomes were closed circular DNA molecules with a set of 37 genes: 13 protein-coding genes (PCGs), 22 tRNA, 2 rRNA, and a non-coding region (Fig. 1). GenBank accession numbers are provided in Suppl. material 3.

Phylogenetic relationships

The analyzed dataset contained 87 terminals and 15,519 aligned positions. Models selected per partition by MODELFINDER are listed in Table 1. The maximum-likelihood tree (log likelihood = −280,549.797) recovered two main clades within *Stenocercus* (Fig. 2): one of Andean and lowland taxa (SH-aLRT = 100, UB = 100) and another of Andean species (SH-aLRT = 99.7, UB = 100). Supraspecific clades (sensu Torres-Carvajal et al. 2006) Anatomegalepis, Boreomegalepis, and Scelotrema are monophyletic. Within Scelotrema, clades Microphractus, Microphractoides, and Saccodeira are also monophyletic.

Stenocercus chrysopygus terminals belong to Saccodeira, a clade that includes another eight Central Andes Peruvian species (SH-aLRT = 100, UB = 100): *S. amydrorhytus*, *S. latebrosus*, *S. johaberfellneri*, *S. melanopygus*, *S. modestus*, *S. orientalis*, *S. ornatissimus*, and *S. stigmosus*.

Samples of *S. chrysopygus* do not form a monophyletic clade (Fig. 2). Clade A (SH-aLRT = 100, UB = 100) includes *S. chrysopygus* samples from the western slope of the Cordillera Blanca and the eastern slope of the Cordillera Negra (Fig. 3). Genetic distances within clade A reached up to 1% for COI and from 2% to 5% for cytb (Table 2). Clade B (SH-aLRT = 100, UB = 100) is composed of samples from the southeastern slope of the Cordillera

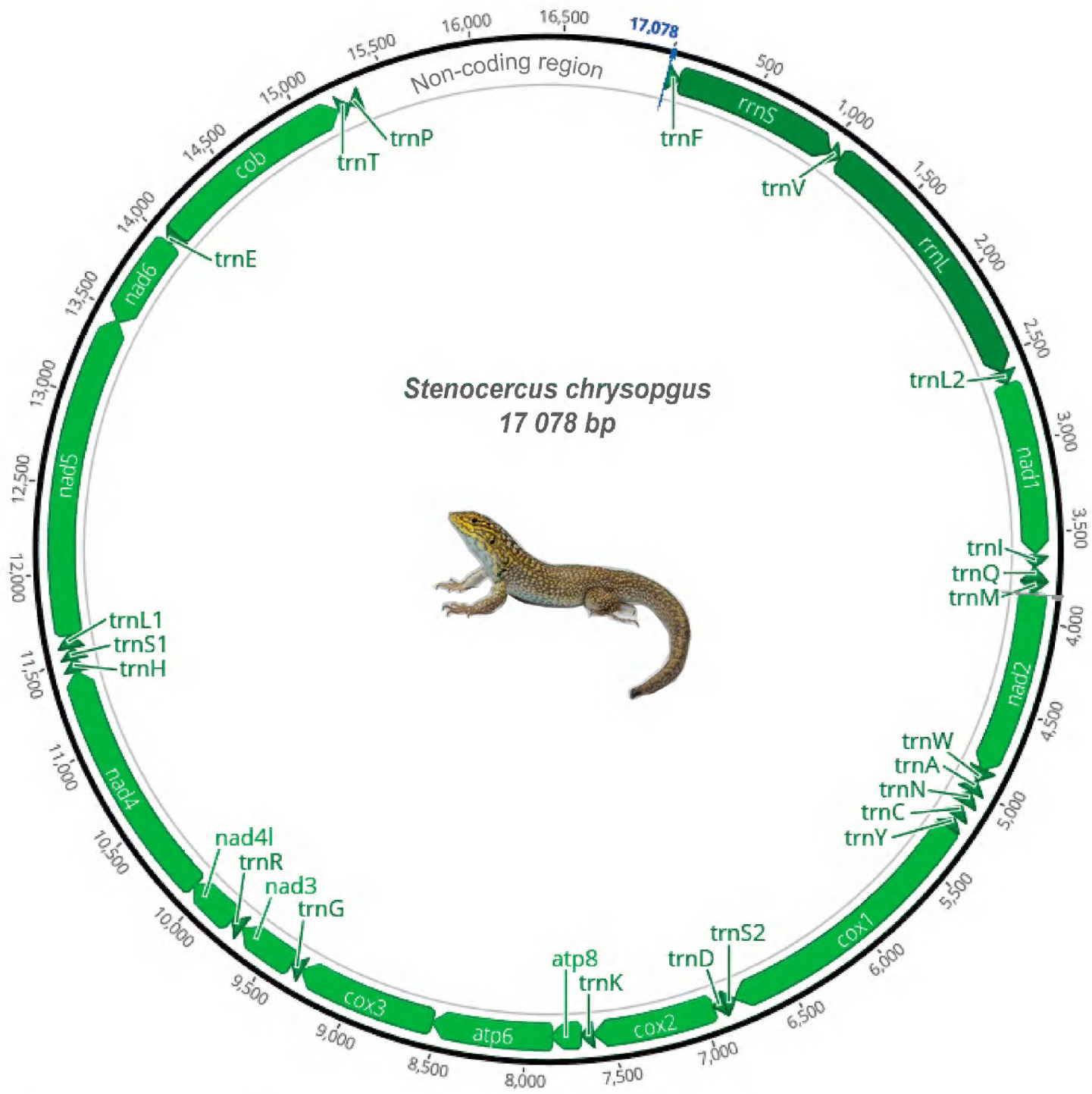

Figure 1. Map of the mitogenome of *Stenocercus chrysopygus*. MUSM 41678 (GenBank accesion number: PX114735).

Table 1. Partition scheme, model, and BIC score per partition scheme selected by ModelFinder.

Partition	Model	BIC
12S, 16S, ND1_2, atp8, ND2, ND6, tRNA-Val, tRNA-Ala, tRNA-Asn, tRNA-Cys, tRNA-Phe, tRNA-Gly, tRNA-Gln, tRNA-Ile, tRNA-Leu1, tRNA-Met, tRNA-Pro, tRNA-Ser1, tRNA-Trp	GTR+F+I+G4	207256.7157
COI_1, COI_2, COX2, COX3, cytb_1, tRNA-Asp, tRNA-Glu, tRNA-His, tRNA-Lys, tRNA-Leu2, tRNA-Arg, tRNA-Ser2, tRNA-Thr	GTR+F+I+G4	122816.0015
NAD3, ND1_1, atp6, cytb2, ND4, ND4l, ND5	GTR+F+I+G4	231487.2086
tRNA-Tyr	TIM3+F+G4	3015.2002

Blanca (Fig. 3), with genetic distances of 1% and 4% for COI and cytb, respectively (Table 2). Clade C (SH-aLRT = 100, UB = 100) includes samples from the northeastern slope of the Cordillera Blanca. Clade D (SH-aLRT = 100, UB = 100) includes samples from the western slope of the Cordillera Negra, is sister to *S. johaberfellneri* (SH-aLRT = 100, UB = 100), and forms part of a clade including *S. amydrorhytus*, *S. modestus*, and *S. ornatissimus*. Genetic distances within clades C and D are 0% for COI and cytb. Genetic distances among these four clades range from 4% to 7% for COI and from 12% to 20% for cytb (Table 2). Genetic distances between clade D and *S. johaberfellneri* are 2% and 5% for COI and cytb, respectively (Table 2).

In the following sections, clade A, which includes all terminals from syntype localities, will be referred to as *Stenocercus chrysopygus* sensu stricto (s.s.). Clades A, B, C, and D, as a group, will be referred to as *Stenocercus chrysopygus* sensu lato.

Species delimitation

For species delimitation analyses, we included all *S. chrysopygus* sensu lato terminals. Additionally, we included *S. amydrorhytus* and *S. johaberfellneri*, the latter is sister to clade D.

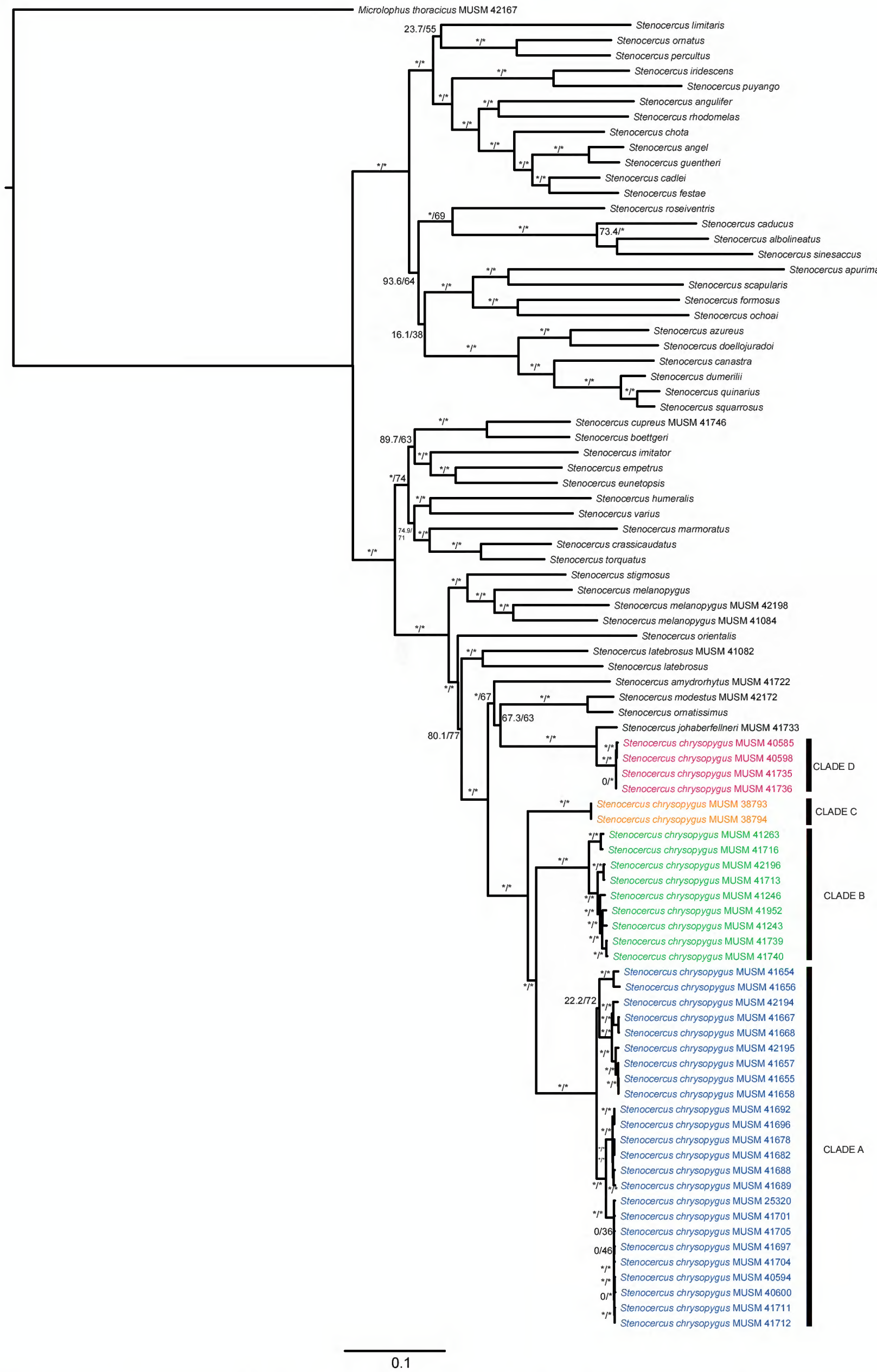

Figure 2. Maximum likelihood tree (log likelihood = -280,549.797) showing phylogenetic relationships of *Stenocercus* inferred from 15,519 aligned positions of 13 mitochondrial PCGs (ATP6, ATP8, CYTB, COX1, COX2, COX3, ND1, ND2, ND3, ND4, ND4L, ND5, ND6). 22 tRNA (trnA, trnC, trnD, trnE, trnF, trnG, trnH, trnI, trnK, trnL1, trnL2, trnM, trnN, trnP, trnQ, trnR, trnS1, trnS2, trnT, trnV, trnW, and trnY) and two rRNA (rrnL and rrnS) genes. Support values SH-aLRT and Ultrafast Bootstrap on the left and right, respectively. UB and SH-aLRT ≥ 95 and 80, respectively, are indicated by an asterisk.

Table 2. Uncorrected p-distances among *Stenocercus chrysopygus* terminals and *S. johaberfellneri*. Upper right values show distances for an 1,137 bp cytb fragment. Lower left values show distances for a 1,545 bp COI fragment.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. *Stenocercus chrysopygus* Clade A MUSM 41704	–	0.0153	0.0429	0.0361	0.0390	0.1501	0.1466	0.1252	0.1252	0.1923	0.1937	0.1889	0.1902
2. *Stenocercus chrysopygus* Clade A MUSM 41678	0.0047	–	0.0428	0.0369	0.0379	0.1473	0.1425	0.1302	0.1302	0.1935	0.1949	0.1885	0.1899
3. *Stenocercus chrysopygus* Clade A MUSM 41656	0.0124	0.0121	–	0.0439	0.0469	0.1473	0.1504	0.1312	0.1312	0.1982	0.1995	0.2043	0.2058
4. *Stenocercus chrysopygus* Clade A MUSM 41668	0.0136	0.0124	0.0135	–	0.0153	0.1406	0.1373	0.1224	0.1224	0.1925	0.1938	0.1804	0.1818
5. *Stenocercus chrysopygus* Clade A MUSM 41655	0.0130	0.0113	0.0118	0.0044	–	0.1446	0.1360	0.1238	0.1238	0.1940	0.1954	0.1823	0.1836
6. *Stenocercus chrysopygus* Clade B MUSM 41740	0.0429	0.0454	0.0470	0.0436	0.0439	–	0.0370	0.1539	0.1539	0.2012	0.2026	0.2051	0.2065
7. *Stenocercus chrysopygus* Clade B MUSM 41716	0.0407	0.0424	0.0455	0.0413	0.0410	0.0064	–	0.1431	0.1431	0.1940	0.1954	0.1959	0.1972
8. *Stenocercus chrysopygus* Clade C MUSM 38794	0.0391	0.0397	0.0433	0.0393	0.0397	0.0400	0.0396	–	0.0000	0.1939	0.1952	0.1918	0.1904
9. *Stenocercus chrysopygus* Clade C MUSM 38793	0.0391	0.0397	0.0433	0.0393	0.0397	0.0400	0.0396	0.0000	–	0.1939	0.1952	0.1918	0.1904
10. *Stenocercus chrysopygus* Clade D MUSM 41736	0.0623	0.0630	0.0671	0.0657	0.0659	0.0657	0.0655	0.0613	0.0613	–	0.0009	0.0497	0.0487
11. *Stenocercus chrysopygus* Clade D MUSM 40585	0.0623	0.0630	0.0671	0.0657	0.0659	0.0657	0.0655	0.0613	0.0613	0.0000	–	0.0506	0.0497
12. *Stenocercus johaberfellneri* MUSM 41733	0.0605	0.0616	0.0672	0.0651	0.0661	0.0631	0.0605	0.0592	0.0592	0.0154	0.0154	–	0.0009
13. *Stenocercus johaberfellneri* MUSM 41734	0.0602	0.0613	0.0668	0.0648	0.0657	0.0627	0.0601	0.0588	0.0588	0.0151	0.0151	0.0003	–

Aligned matrices of COI (1,545 bp) and cytb (1,137 bp) were analyzed using ASAP. The best partition for COI and cytb analyses included four species hypotheses among *S. chrysopygus* sensu lato terminals: clades A, B, C, and D (Fig. 4). We conducted tree searches for the concatenated matrix of COI and cytb sequences, as well as for each matrix separately. Trees from the concatenated and cytb matrices recovered the same topology, with lower support in the cytb tree. The COI matrix analysis recovered a tree with the same main clades but some different relationships with low support (results not shown). The tree from the concatenated analysis, which had more information and higher support values, was used in the bPTP analysis. The bPTP analysis inferred eight species hypotheses among *S. chrysopygus* sensu lato terminals (Fig. 4). Three hypotheses included clade A terminals; clades B and C were each divided into two hypotheses, and clade D was inferred as a single hypothesis (Suppl. material 4). None of the eight hypotheses had support above 0.91 (Suppl. material 4). Both bPTP and ASAP analyses identified *S. amydrorhy-*

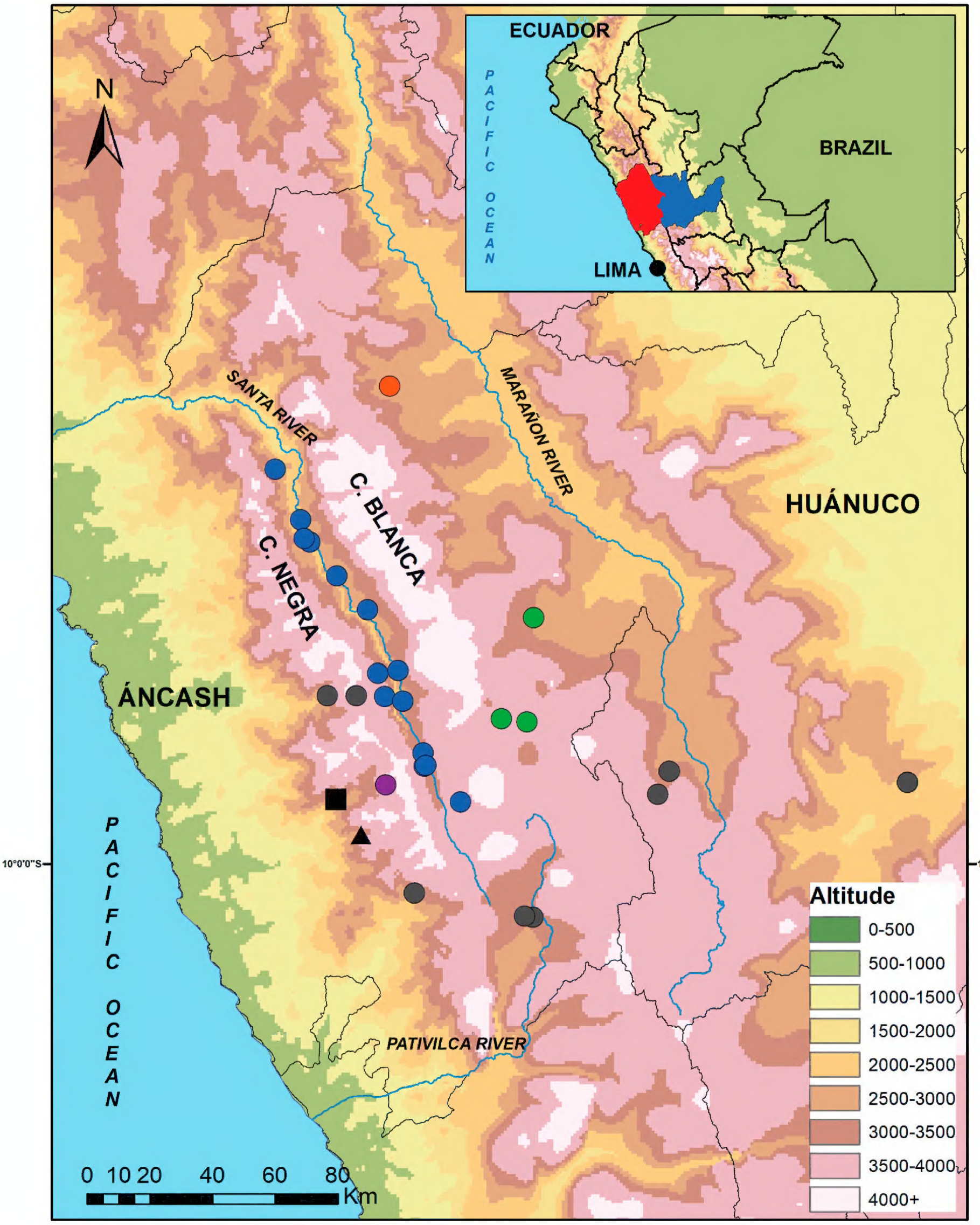

Figure 3. Distribution of *Stenocercus chrysopygus* (circles), *S. amydrorhytus* (square), and *S. johaberfellneri* (triangle). *Stenocercus chrysopygus* samples are colored by clade: Clade A (blue), Clade B (green), Clade C (orange), and Clade D (purple). *Stenocercus chrysopygus* localities without DNA sequences are represented by gray circles. The inset map highlights the Áncash (red) and Huánuco (blue) departments in central Peru.

tus and *S. johaberfellneri* as well-supported hypotheses (Suppl. material 4).

The method with the highest Relative Taxonomic Resolving Power Index was bPTP (Rtax = 1), whereas ASAP estimations with COI and cytb had Rtax = 0.6. The high Rtax of bPTP reflects overestimation of hypotheses by placing terminals from the same locality in different hypotheses for clades A, B, C, and D. ASAP estimations with COI and cytb had Ctax = 1, as both resulted in the same species hypotheses. Ctax calculations of ASAP relative to bPTP were 0.6.

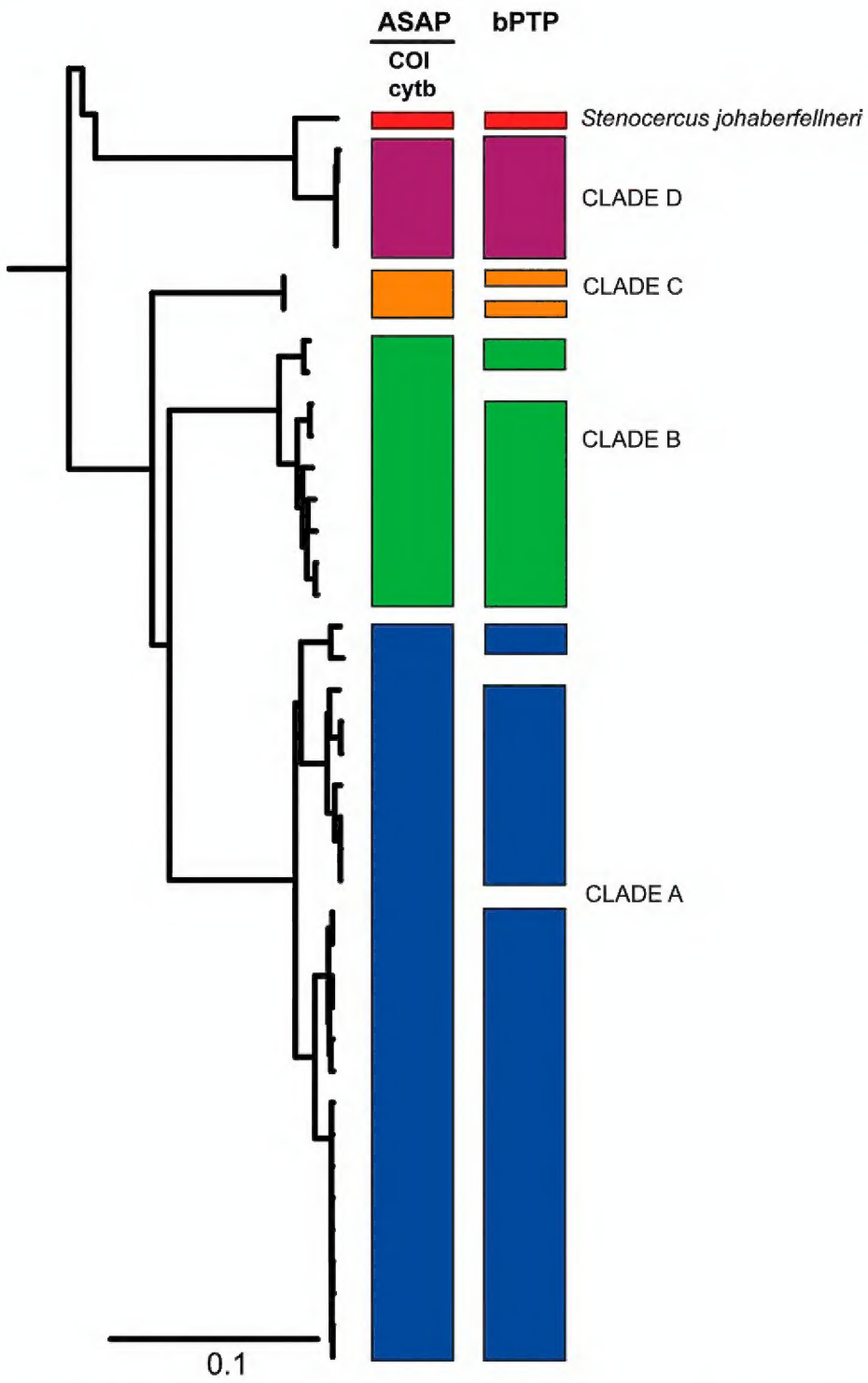

Figure 4. Results from the species delimitation methods analyses. Bars of the same color indicate conspecific samples according to each of the methods. The topology of the ML tree, based on the analysis of 13 mitochondrial PCGs, 22 tRNA, and two rRNA, was trimmed to show the section including *Stenocercus chrysopygus* sensu lato and *S. johaberfellneri*. Aligned matrices of COI (1,545 bp) and cytb (1,137 bp) were analyzed independently and concatenated for ASAP and bPTP analyses, respectively.

DFA analyses

The DFA analysis of meristic data correctly classified 56 (44%) specimens of *S. chrysopygus* s.s. (Table 3). The remaining 70 specimens were almost equally classified as either clade C or clade D, one as clade B, and 12 as *Stenocercus johaberfellneri*. From clade B, 40 specimens (98%) were correctly classified, and one was assigned to clade C. The two clade C specimens were correctly classified. Two (50%) clade D specimens were correctly classified, and two were assigned each to *S. chrysopygus* s.s. and clade C. All *S. johaberfellneri* specimens were correctly classified. In the multivariate space, the *S. chrysopygus* s.s. convex hull overlapped data from all other clades and *S. johaberfellneri* (Fig. 5A). However, clade B is differentiated from all groups, with slight overlap with the clade A convex hull, and clade D and *S. johaberfellneri* are also differentiated (Fig. 5A).

A PCA of morphometric data did not separate data by sex, so all morphometric data were pooled. Among 146 *S. chrysopygus* s.s. specimens, 33 (23%) were correctly classified. The remaining specimens were almost equally assigned to clades B, D, and *S. johaberfellneri*, except for two assigned to clade C (Table 4). Eleven (52%) of 21 specimens from clade B were correctly classified. The remaining specimens were classified as clade D, *S. chrysopygus* s.s., or *S. johaberfellneri*. One specimen from clade C was correctly classified, and the other was assigned to clade B. Three of four specimens (75%) from clade D were correctly classified, and one was classified as clade B. All *S. johaberfellneri* specimens were correctly classified. The *S. chrysopygus* convex hull overlapped data from all other clades and *S. johaberfellneri* (Fig. 5B). Both *S. johaberfellneri* and clade D convex hulls overlapped clade B data; however, their convex hulls were differentiated (Fig. 5B). One specimen from clade C and three *S. chrysopygus* s.s. specimens were outliers (Fig. 5B).

Gap analyses

We compared meristic and morphometric data between two pairs of sister clades: *S. chrysopygus* s.s. and clade B, and clade D and *S. johaberfellneri*, respectively. Clade C could not be included because only two adult specimens were available.

Although comparisons for meristic data between *S. chrysopygus* s.s. and clade B, and clade D and *S. johaberfellneri*, showed separation in the multivariate space and resulted in bimodal plots along the ridgeline manifold (Fig. 6A, B, D, E), the overlap of tolerance regions did not exceed the frequency cutoff of 0.1 (Fig. 6C, F). However, the overlap of tolerance regions in the clade B and *S. chrysopygus* s.s. analysis almost exceeded the frequency cutoff (Fig. 6C).

A PCA of morphometric data of males and females did not separate data by sex, so all morphometric data for each group were pooled. Comparison between *S. chrysopygus* s.s. and clade B showed overlap in the multivariate space and resulted in a unimodal plot (Fig. 7A, B). Comparison between clade D and *S. johaberfellneri* showed separation in the multivariate space and resulted in a bimodal plot. However, the overlap of tolerance regions did not exceed the frequency cutoff of 0.1 (Fig. 7C–E).

Qualitative characters

Table 5 summarizes the main qualitative differences among *S. chrysopygus* s.s., *S. johaberfellneri*, and clades B, C, and D. These include the color pattern of adult males, shape and relief of nuchal scales, and depth of the oblique neck fold (Figs 8, 9). Adult males of *S. chrysopygus* s.s. have a bright yellow patch from the lower half of the chest, hourglass-shaped over the venter, and continuous to the pelvic region, thighs, and shanks (Fig. 8A).

Table 3. Confusion matrix of the DFA analysis of meristic data from specimens from four clades identified among *Stenocercus chrysopygus* sensu lato samples and *S. johaberfellneri*.

	1	2	3	4	5	Total
1. *S. chrysopygus* s.s (Clade A)	56	1	23	34	12	126
2. Clade B	0	40	1	0	0	41
3. Clade C	0	0	2	0	0	2
4. Clade D	1	0	1	2	0	4
5. *S. johaberfellneri*	0	0	0	0	5	5
Total	57	41	27	36	17	178

Table 4. Confusion matrix of the DFA analysis of morphometric data from specimens from four clades identified among *Stenocercus chrysopygus* sensu lato samples and *S. johaberfellneri*.

	1	2	3	4	5	Total
1. *S. chrysopygus* s.s (Clade A)	33	35	2	29	47	146
2. Clade B	4	11	0	4	2	21
3. Clade C	0	1	1	0	0	2
4. Clade D	0	1	0	3	0	4
5. *S. johaberfellneri*	0	0	0	0	4	4
Total	37	48	3	36	53	177

Table 5. Comparison of qualitative characters among *Stenocercus chrysopygus* s.s., clades B, C, D, and *S. johaberfellneri*.

Character	*Stenocercus chrysopygus* s.s	Clade B	Clade C	Clade D	*Stenocercus johaberfellneri*
1. Bright yellow patch from lower half of chest, hourglass shaped over venter, and continuous to pelvic region, thighs and shanks in adult males	Present	Absent	Absent	Absent	Absent
2. Throat with reticulated pattern in adult males	Present	Absent	Present	Absent	Present
3. Flanks background color orange	Present	Absent	Absent	Present	Absent
4. Lateral nuchals less than one-fourth dorsal nuchals, subimbricate, slightly larger and weakly keeled over longitudinal, oblique and antehumeral folds	Present	Absent	Present	Absent	Absent
5. Shallow oblique neck fold	Present	Present	Present	Absent	Absent

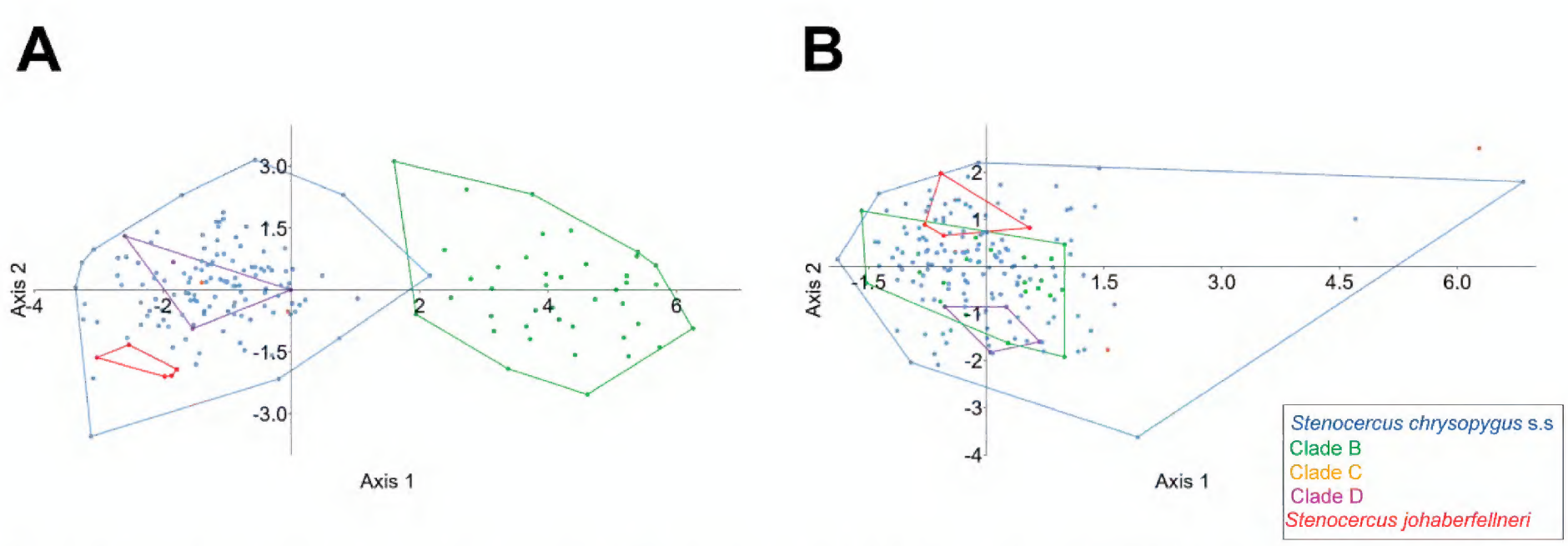

Figure 5. Scatterplots, including the first two axes, of DFA of meristic (**A**) and morphometric data (**B**). Convex hulls delimit groups representing clades depicted in Fig. 2 and *Stenocercus johaberfellneri*. Blue: *S. chrysopygus* s.s., Green: Clade B, Orange: Clade C, Purple: Clade D, Red: *S. johaberfellneri*.

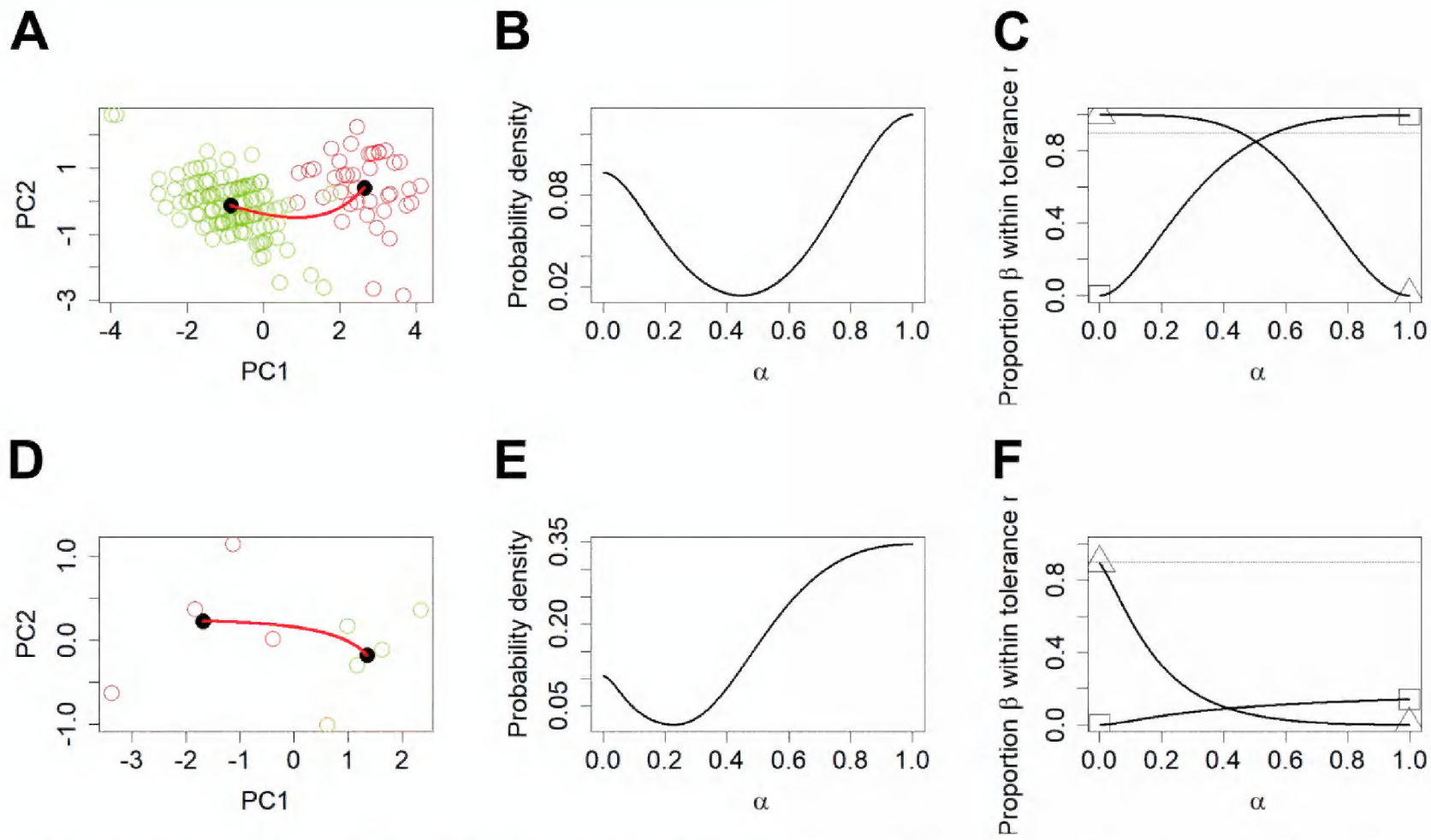

Figure 6. Graphic results of gap analyses of meristic data. PCA (**A, D**), estimated probability density function (x) for various points along the ridgeline manifold (y) (**B, E**), and estimated beta proportion covered by tolerance regions (**C, F**). Clade B vs. *Stenocercus chrysopygus* s.s. (top), Clade D vs. *S. johaberfellneri* (bottom).

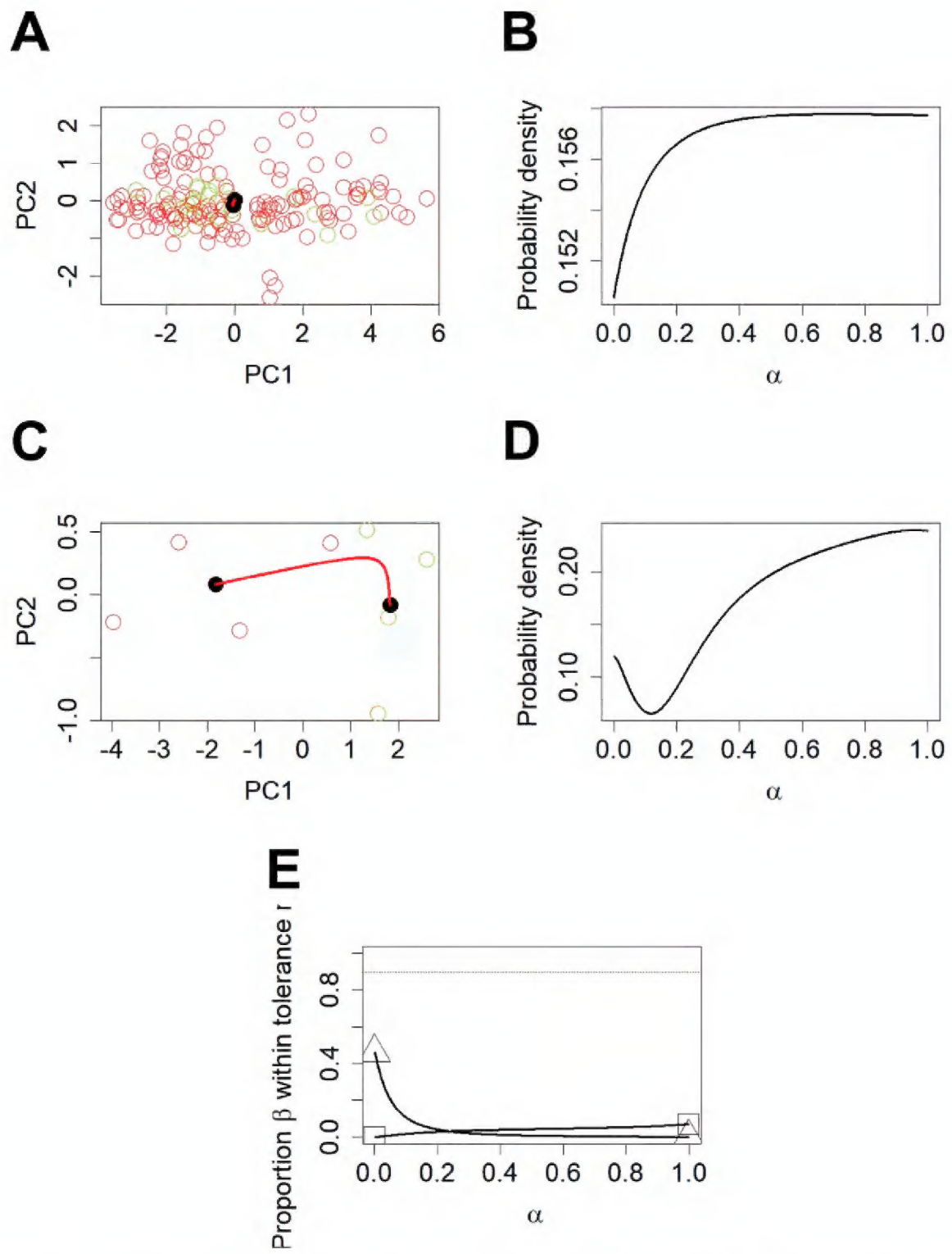

Figure 7. Graphic results of gap analyses of morphometric data. PCA (**A, C**), the estimated probability density function (x) for various points along the ridgeline manifold (y) (**B, D**), and the estimated beta proportion covered by tolerance regions (**E**). *Stenocercus chrysopygus* s.s. vs. Clade B (**A, B**), Clade D vs. *S. johaberfellneri* (**C, D, E**).

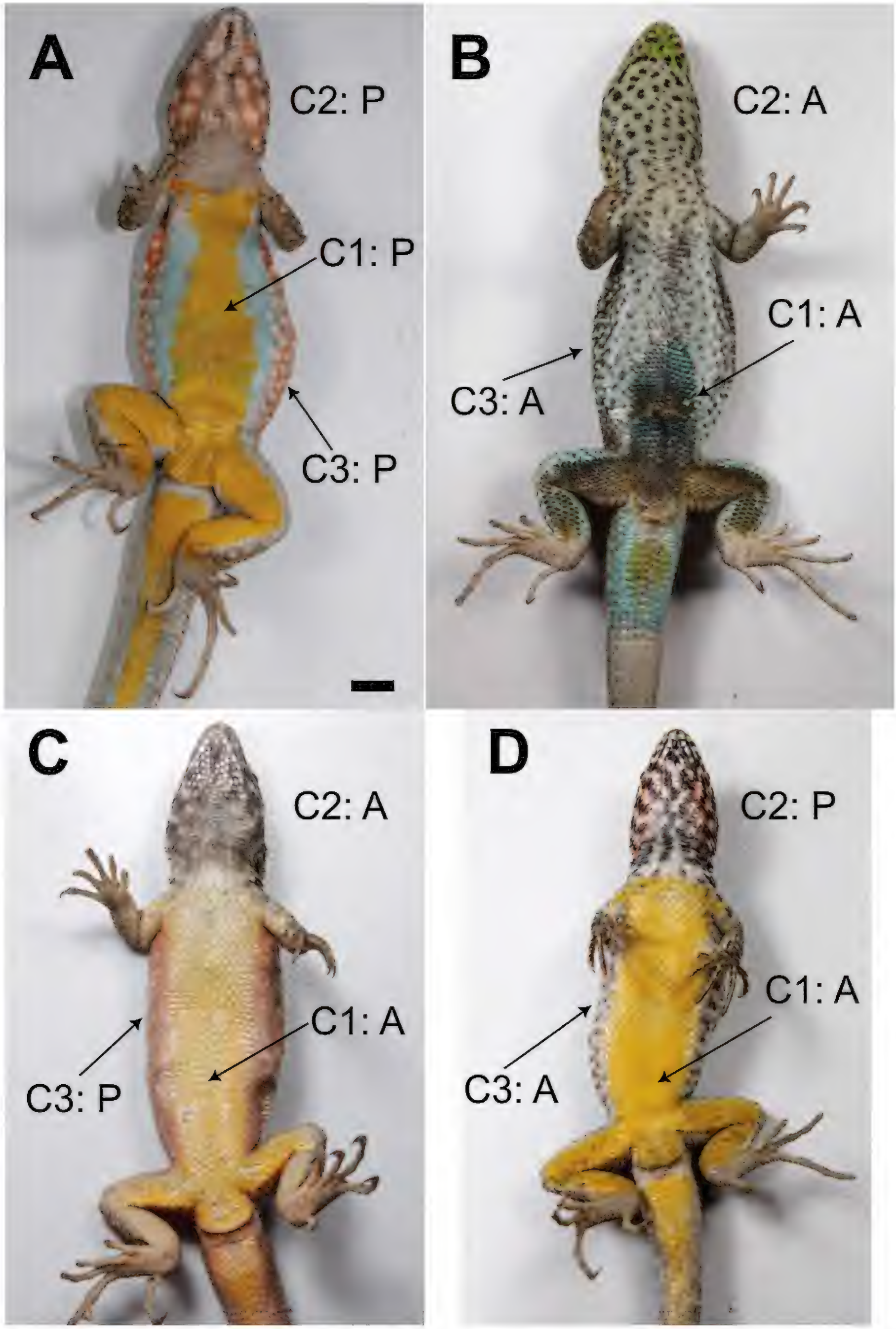

Figure 8. Ventral view of adult males of *Stenocercus chrysopygus* s.s. (MUSM 41657) (**A**), Clade B (MUSM 41714) (**B**), Clade D (MUSM 41735) (**C**), and *S. johaberfellneri* (MUSM 41734) (**D**). Photographs depict characters 1–3 from Table 5. A – Absent, P – Present. Scale bar: 1 mm.

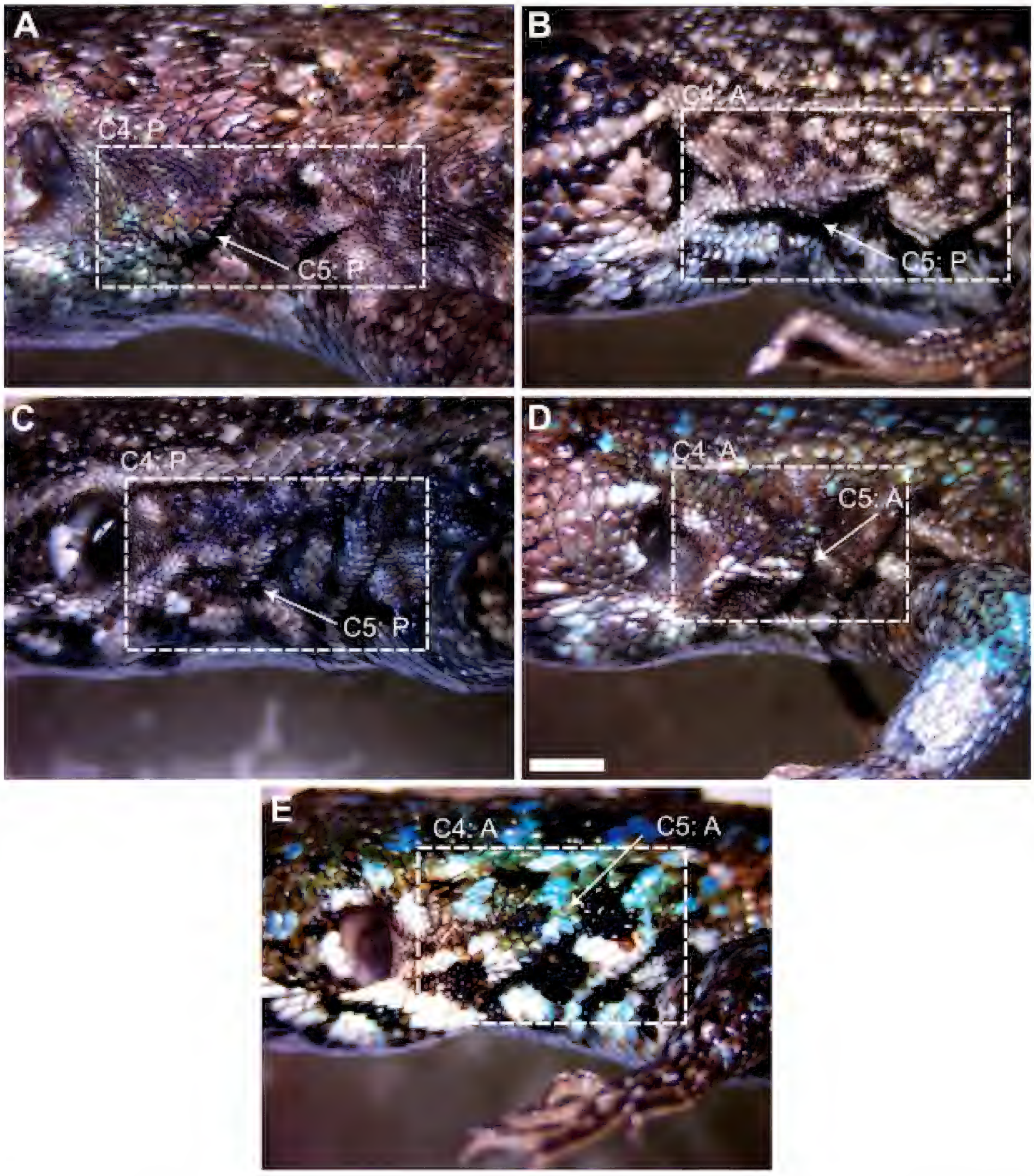

Figure 9. Lateral view of the neck of adult males of *Stenocercus chrysopygus* sensu lato and *S. johaberfellneri*. **A.** *Stenocercus chrysopygus* s.s. (MUSM 41695); **B.** Clade B (MUSM 41714); **C.** Clade C (MUSM 38793); **D.** Clade D (MUSM 41735); and **E.** *S. johaberfellneri* (MUSM 41729). Photographs depict characters 4 and 5 from Table 5. A – Absent, P – Present. Scale bar: 1 mm.

This coloration pattern is absent in clades B, C, D, and *S. johaberfellneri* (Fig. 8B–D). Adult males from clades B (Fig. 8B) and C have black ventral coloration. Clade D and *S. johaberfellneri* males have completely yellow venters (Fig. 8C, D). An orange background coloration on the flanks is present in *S. chrysopygus* s.s. and clade D (Fig. 8A, C). Clade B and *S. johaberfellneri* have cream background coloration on the flanks (Fig. 8B, D). Another coloration character distinctive of *S. chrysopygus* s.s., clade C, and *S. johaberfellneri* adult males is a reticulated pattern on the throat (Fig. 8A, D). This pattern is absent in adult males from clades B and D (Fig. 8B, C). Lateral nuchals of specimens from *S. chrysopygus* s.s. (Fig. 9A) and clade C (Fig. 9C) are less than one-fourth dorsal nuchals, subimbricate, slightly larger, and weakly keeled over longitudinal, oblique, and antehumeral folds,

contrasting with granular scales in clade B (Fig. 9B) and keeled scales in clade D (Fig. 9D) and *S. johaberfellneri* (Fig. 9E). Finally, specimens from *S. chrysopygus* s.s., clade B, and clade C have a shallow oblique neck fold (Fig. 9A–C), whereas clade D and *S. johaberfellneri* have deep oblique neck folds (Fig. 9D, E).

Discussion

Stenocercus chrysopygus systematics

Our study addressed a longstanding taxonomic question raised for half a century (Fritts 1974; Cadle 1998; Torres-Carvajal 2007a): Do *Stenocercus chrysopygus* populations include more than one species? We provide a mitogenome-based phylogenetic hypothesis and a DNA barcode-based species partitioning to propose primary species hypotheses (PSH, sensu Miralles et al. 2024). PSH were confronted with external morphological traits and patterns of geographic isolation from several *S. chrysopygus* populations to propose secondary species hypotheses (SSH, sensu Miralles et al. 2024). Our phylogenetic hypothesis includes four reciprocally monophyletic clades of *S. chrysopygus* terminals (clades A, B, C, and D). Considering our mitogenome phylogeny and DNA barcode-based species partitioning, we propose clades B, C, and D as PSH. Clade A, including samples from all syntype localities, corresponds to *S. chrysopygus* s.s. The ASAP and bPTP species delimitation methods resulted in four and eight PSH, respectively, among *S. chrysopygus* samples. Although bPTP oversplit clades (e.g., the two samples from clade C, from the same locality, were considered two different species hypotheses), the delimitation of three species hypotheses within *S. chrysopygus* s.s. could be supported by the wide distribution of these terminals in the Santa River valley and the genetic structure corresponding with geographic location. However, examined specimens from different localities fall within a shared range of morphological variation, supporting *S. chrysopygus* s.s. as a single lineage. Similarly, bPTP delimits two species hypotheses within clade B. However, the delimited groups share samples from the same localities, so clade B is also considered a single lineage. On the other hand, ASAP delimitation is consistent with phylogenetic and morphological evidence. Both ASAP and bPTP supported the clade D and *S. johaberfellneri* as distinct species hypotheses.

Each clade has diagnostic meristic and qualitative characters and is geographically isolated, mainly by mountain ranges such as the Cordillera Blanca and Cordillera Negra. Although there is no strict morphological gap in scale counts, clade B has 98% of individuals correctly assigned in the meristic DFA analysis and higher counts of scales around the midbody, vertebral scales, and paravertebral scales, as remarked by Fritts (1974) for populations from the eastern slope of the Cordillera Blanca. Among qualitative characters, the ventral coloration of adult males differentiates *S. chrysopygus* s.s. from *S. johaberfellneri* and clades B, C, and D. Black ventral coloration is present in adult males from clades B and C, a characteristic previously highlighted for populations east of the Cordillera Blanca (Fritts 1974). Finally, the shape and relief of lateral nuchals and the depth of the oblique neck fold differentiate *S. chrysopygus* s.s. and clades B and C from *S. johaberfellneri* and clade D. Clade D and its sister species, *S. johaberfellneri*, were differentiated by DFA analyses of meristic and morphometric data. On the other hand, the gap analysis of meristic data of clade D and *S. johaberfellneri* resulted in a bimodal distribution of the data; however, the final conclusion of the analysis rejected species-level differentiation. Qualitatively, these clades are differentiated by the background color on the flanks of adult males and the coloration pattern on the throat. Considering both molecular and morphological evidence, the differentiation of clade D and *S. johaberfellneri* is supported.

Other *Stenocercus chrysopygus* populations

Two populations historically assigned to *S. chrysopygus* remain unsampled for genetic data: 5 km NE of La Unión and Chiquián in Huánuco and Áncash, respectively (Fritts 1974; Torres-Carvajal 2007a). We visited the 5 km NE of La Unión locality with no capture success. We saw one lizard running across a path and a second individual on a rock along a path with abundant *Agave*. The La Unión locality is highly fragmented, with vast unshaded agricultural areas. The Chiquián population is located south of the Cordillera Blanca, in the valley of the Chiquián River, a tributary of the Pativilca River. Unfortunately, Chiquián was not included in our expedition.

Cadle (1998) discussed the morphological differences of samples from 31 km (by road) E of Pariacoto, 1 km N and 12 km E of Pariacoto, and Marca, in western Áncash, with *S. chrysopygus* and *S. ornatissimus*. These populations remain in an ambiguous classification. Cadle (1998) hypothesized that these correspond to geographic variants of either *S. chrysopygus* or *S. ornatissimus*. We visited 31 km (by road) E of Pariacoto but found only one specimen of *Liolaemus chavin* Aguilar et al., 2013. Cadle (1998) also included specimens from Bosque de Zapatagocha and Aguamiro, in Huánuco, as *S. chrysopygus*. These localities were not sampled in our expedition. While Aguamiro is about 8 km southwest of 5 km NE of La Unión, Bosque de Zapatagocha lies on the eastern slope of the Cordillera Oriental.

Although the phylogenetic relationships and species boundaries of all the aforementioned populations need to be addressed following an integrative framework (Aguilar et al. 2013), we can affirm that none of them corresponds to *S. chrysopygus* s.s. We have access to specimens from 5 km NE of La Unión and Chiquián, and their taxonomic status will be addressed in an upcoming article. Unfortunately, so far, we have not examined specimens from the other five localities.

Phylogenetic relationships of *Stenocercus*

Our phylogenetic analysis recovered two main *Stenocercus* clades, as in previous studies (Torres-Carvajal 2007b; Teixeira et al. 2016). Compared to the most recent molecular phylogeny of the genus (Teixeira et al. 2016), our dataset includes more terminals and characters. We also applied a different optimality criterion, which resulted in some differences in the inferred phylogenetic relationships. Within Scelotrema, our results recovered Saccodeira as sister to all other terminals. In the clade including Andean and lowland taxa, Anatomegalepis was sister to a clade of species from the Atlantic lowlands and Amazon Basin. Future studies including more taxa, nuclear genes, and morphological characters, using the Torres-Carvajal (2007b) matrix as a starting point, will contribute greatly to the study of the evolutionary history of *Stenocercus*.

Conclusion

Our results support the hypothesis of Fritts (1974) that populations from different elevations along the Santa River valley in the Áncash department are a single lineage corresponding to *Stenocercus chrysopygus* s.s. Three SSH are proposed among *S. chrysopygus* sensu lato populations: two from the eastern Cordillera Blanca and one from the western slope of the Cordillera Negra. A taxonomic revision of *S. chrysopygus*, including the formal description of SSH, will be presented in upcoming articles.

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References

Aguilar C, Wood Jr PL, Cusi JC, Guzman A, Huari F, Lundberg M, Mortensen E, Ramírez C, Robles D, Suárez J, Ticona A, Vargas VJ, Venegas PJ, Sites Jr JW (2013) Integrative taxonomy and preliminary assessment of species limits in the *Liolaemus walkeri* complex (Squamata, Liolaemidae) with descriptions of three new species from Peru. ZooKeys 364: 47–91. https://doi.org/10.3897/zookeys.364.6109

Al Arab M, Höner zu Siederdissen C, Tout K, Sahyoun AH, Stadler PF, Bernt M (2017) Accurate annotation of protein-coding genes in mitochondrial genomes. Molecular Phylogenetics and Evolution 106: 209–216. https://doi.org/10.1016/j.ympev.2016.09.024

Andrews S (2010) FastQC: a quality control tool for high throughput sequence data. http://www.bioinformatics.babraham.ac.uk/projects/fastqc/

Bivand R, Wong D (2018) Comparing implementations of global and local indicators of spatial association. Test 27(3): 716–748. https://doi.org/10.1007/s11749-018-0599-x

Boulenger GA (1885) Catalogue of the Lizards in the British Museum (Natural History), Volume 2. Taylor and Francis, London, U.K.

Boulenger GA (1900) Descriptions of new batrachians and reptiles collected by Mr. P.O. Simons in Peru. Annals & Magazine of Natural History 6(32): 181–186. https://doi.org/10.1080/00222930008678355

Cadle JE (1998) New species of lizards, genus *Stenocercus* (Iguania: Tropiduridae), from western Ecuador and Peru. Bulletin of the Museum of Comparative Zoology 155: 257–297.

Carvalho AL, Rivas LR, Céspedes R, Rodrigues MT (2018) A new collared lizard (*Tropidurus*: Tropiduridae) endemic to the Western Bolivian Andes and its implications for seasonally dry tropical forests. American Museum Novitates 2018(3896): 1–56. https://doi.org/10.1206/3896.1

Chen S, Zhou Y, Chen Y, Gu J (2018) fastp: An ultra-fast all-in-one FASTQ preprocessor. Bioinformatics (Oxford, England) 34(17): i884–i890. https://doi.org/10.1093/bioinformatics/bty560

Chernomor O, Von Haeseler A, Minh BQ (2016) Terrace aware data structure for phylogenomic inference from supermatrices. Systematic Biology 65(6): 997–1008. https://doi.org/10.1093/sysbio/syw037

Donath A, Jühling F, Al-Arab M, Bernhart SH, Reinhardt F, Stadler PF, Middendorf M, Bernt M (2019) Improved annotation of protein-coding genes boundaries in metazoan mitochondrial genomes. Nucleic Acids Research 47(20): 10543–10552. https://doi.org/10.1093/nar/gkz833

Fritts TH (1974) A multivariate and evolutionary analysis of the Andean iguanid lizards of the genus *Stenocercus*. San Diego Society of Natural History Memoir 7: 1–89.

Frost DR, Crafts HM, Fitzgerald LA, Titus TA (1998) Geographic variation, species recognition, and molecular evolution of cytochrome oxidase I in the *Tropidurus spinulosus* complex (Iguania: Tropiduridae). Copeia 1998(4): 839–851. https://doi.org/10.2307/1447331

Genz A, Bretz F (2009) Computation of Multivariate Normal and t Probabilities, series Lecture Notes in Statistics. Springer-Verlag, Heidelberg. https://doi.org/10.1007/978-3-642-01689-9

Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. Systematic Biology 59(3): 307–321. https://doi.org/10.1093/sysbio/syq010

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics software package for education and data analysis. Palaeontologia Electronica 4(1): 1–9.

Hoang DT, Chernomor O, Von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the ultrafast bootstrap approximation. Molecular Biology and Evolution 35(2): 518–522. https://doi.org/10.1093/molbev/msx281

Jin JJ, Yu WB, Yang JB, Song Y, DePamphilis CW, Yi TS, Li DZ (2020) GetOrganelle: A fast and versatile toolkit for accurate de novo assembly of organelle genomes. Genome Biology 21(1): 1–31. https://doi.org/10.1186/s13059-020-02154-5

Kalyaanamoorthy S, Minh BQ, Wong TK, Von Haeseler A, Jermiin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. Nature Methods 14(6): 587–589. https://doi.org/10.1038/nmeth.4285

Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20(4): 1160–1166. https://doi.org/10.1093/bib/bbx108

Köhler G, Lehr E (2015) Two new species of lizards of the genus *Stenocercus* (Iguania, Tropiduridae) from central Peru. Zootaxa 3956(3): 413–427. https://doi.org/10.11646/zootaxa.3956.3.6

Kuraku S, Zmasek CM, Nishimura O, Katoh K (2013) aLeaves facilitates on-demand exploration of metazoan gene family trees on MAFFT sequence alignment server with enhanced interactivity. Nucleic Acids Research 41(W1): W22–W28. https://doi.org/10.1093/nar/gkt389

Larsson A (2014) AliView: A fast and lightweight alignment viewer and editor for large data sets. Bioinformatics (Oxford, England) 30(22): 3276–3278. https://doi.org/10.1093/bioinformatics/btu531

Mendoza A, Ramírez C, Barrera D, Aguilar-Puntriano C (2021) A new species of the genus *Stenocercus* (Iguania: Tropiduridae) from the Peruvian Pacific coast (Ica region). Salamandra (Frankfurt) 57(1): 1–14.

Minh BQ, Nguyen MAT, Von Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution 30(5): 1188–1195. https://doi.org/10.1093/molbev/mst024

Miralles A, Vences M (2013) New metrics for comparison of taxonomies reveal striking discrepancies among species delimitation methods in *Madascincus* lizards. PLoS One 8(7): e68242. https://doi.org/10.1371/journal.pone.0068242

Miralles A, Puillandre N, Vences M (2024) DNA Barcoding in Species Delimitation: From Genetic Distances to Integrative Taxonomy. In: DeSalle R (Ed.) DNA Barcoding. Methods in Molecular Biology, vol 2744. Humana, New York, NY. https://doi.org/10.1007/978-1-0716-3581-0_4

Murdoch D, Chow ED (2023) ellipse: Functions for Drawing Ellipses and Ellipse-Like Confidence Regions. https://dmurdoch.github.io/ellipse/

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Borman T, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2025) vegan: Community Ecology Package. R package version 2.7-0. https://vegandevs.github.io/vegan/

Posit team (2024) RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. http://www.posit.co/

Puillandre N, Brouillet S, Achaz G (2021) ASAP: Assemble species by automatic partitioning. Molecular Ecology Resources 21(2): 609–620. https://doi.org/10.1111/1755-0998.13281

Roberts DW (2023) labdsv: Ordination and Multivariate Analysis for Ecology. R package version 2.1-0. https://CRAN.R-project.org/package=labdsv

Schlüter U (1999) Pflege und Zucht von *Stenocercus chrysopygus* Boulenger 1900-einem Hochland-Andenkielschwanzleguan aus Peru. Iguana Rundschreiben 12(21): 18–24.

Schlüter U (2000) Bemerkungen zum Status der Populationen von *Stenocercus chrysopygus*. Iguana Rundschreiben 13(23): 29–33.

Schlüter U (2001) Anden-Kielschwanzleguan. Vorkommen, Beschreibung sowie Pflege und Zucht von *Stenocercus chrysopygus*. Aqua (Neu-Isenburg, Germany) 379: 68–70.

Schlüter U (2005) Haltung und Zucht einiger Anden-Kielschwanzleguane *Stenocercus*) aus dem peruanischen Hochland. 5. Ergänzende Bemerkungen zu Stenocercus chlorostictus, zur Jugendfärbung von *Stenocercus empetrus* und zur Variabilität von *Stenocercus chrysopygus*. Reptilia 10(3): 56–63.

Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular evolutionary genetics analysis version 11. Molecular Biology and Evolution 38(7): 3022–3027. https://doi.org/10.1093/molbev/msab120

Teixeira Jr M, Prates I, Nisa C, Silva-Martins NSC, Strüssmann C, Rodrigues MT (2016) Molecular data reveal spatial and temporal patterns of diversification and a cryptic new species of lowland *Stenocercus* Duméril & Bibron, 1837 (Squamata: Tropiduridae). Molecular Phylogenetics and Evolution 94: 410–423. https://doi.org/10.1016/j.ympev.2015.09.010

Torres-Carvajal O (2000) Ecuadorian lizards of the genus *Stenocercus* (Squamata: Tropiduridae). Scientific Papers (University of Kansas. Natural History Museum) 15: 1–38. https://doi.org/10.5962/bhl.title.16286

Torres-Carvajal O (2007a) A taxonomic revision of South American *Stenocercus* (Squamata: Iguania) lizards. Herpetological Monograph 21(1): 76–178. https://doi.org/10.1655/06-001.1

Torres-Carvajal O (2007b) Phylogeny and biogeography of a large radiation of Andean lizards (Iguania, *Stenocercus*). Zoologica Scripta 36(4): 311–326. https://doi.org/10.1111/j.1463-6409.2006.00284.x

Torres-Carvajal O, Mafla-Endara P (2013) A new cryptic species of *Stenocercus* (Squamata: Iguanidae) from the Andes of Ecuador. Journal of Herpetology 47(1): 184–190. https://doi.org/10.1670/11-211

Torres-Carvajal O, Schulte JA II, Cadle JE (2006) Phylogenetic relationships of South American lizards of the genus *Stenocercus* (Squamata: Iguania): a new approach using a general mixture model for gene sequence data. Molecular Phylogenetics and Evolution 39(1): 171–185. https://doi.org/10.1016/j.ympev.2005.09.007

Trifinopoulos J, Nguyen LT, von Haeseler A, Minh BQ (2016) W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Research 44(W1): W232–W235. https://doi.org/10.1093/nar/gkw256

Uetz P, Freed P, Aguilar R, Kudera J, Hošek J [Eds] (2025) The Reptile Database. http://www.reptile-database.org [accessed April 2025]

Vaidya G, Lohman DJ, Meier R (2011) SequenceMatrix: Concatenation software for the fast assembly of multi-gene datasets with character set and codon information. Cladistics 27(2): 171–180. https://doi.org/10.1111/j.1096-0031.2010.00329.x

Venegas PJ, Echevarría LY, Álvarez SC (2014) A new species of spiny-tailed iguanid lizard (Iguania: *Stenocercus*) from northwestern Peru. Zootaxa 3753(1): 047–058. https://doi.org/10.11646/zootaxa.3753.1.4

Venegas PJ, Echevarría LY, García-Burneo K, Koch C (2016) A new species of iguanid lizard, genus *Stenocercus* (Squamata, Iguania), from the Central Andes in Peru. Zootaxa 4205(1): 052–064. https://doi.org/10.11646/zootaxa.4205.1.4

Venegas PJ, Echevarría LY, García-Ayachi LA, Landauro CZ (2020a) Two new sympatric species of *Stenocercus* (Squamata: Iguania) from the inter-Andean valley of the Mantaro River, Peru. Zootaxa 4858(4): 555–575. https://doi.org/10.11646/zootaxa.4858.4.5

Venegas PJ, García-Ayachi LA, Chávez-Arribasplata JC, Chávez G, Wong I, García-Bravo A (2020b) Four new species of *Stenocercus* Duméril & Bibron, 1837 (Squamata, Iguania) from the Department of Amazonas in northeastern Peru. Evolutionary Systematics 4(2): 79–108. https://doi.org/10.3897/evolsyst.4.57578

Venegas PJ, García-Ayachi LA, Chávez-Arribasplata JC, García-Bravo A (2022) Four new species of polychromatic spiny-tailed iguanian lizards, genus *Stenocercus* (Iguania: Tropiduridae), from Peru. Zootaxa 5115(1): 1–28. https://doi.org/10.11646/zootaxa.5115.1.1

Tschudi von JJ (1845) Reptilium conspectum quae in republica Peruana reperiuntur er pleraque observata vel collecta sunt in itenere. Archiv für Naturgeschichte 11(1): 150–170. https://doi.org/10.5962/bhl.part.7963

Wick RR, Schultz MB, Zobel J, Holt KE (2015) Bandage: Interactive visualization of *de novo* genome assemblies. Bioinformatics (Oxford, England) 31(20): 3350–3352. https://doi.org/10.1093/bioinformatics/btv383

Zapata F, Jiménez I (2012) Species delimitation: Inferring gaps in morphology across geography. Systematic Biology 61(2): 179–194. https://doi.org/10.1093/sysbio/syr084

Zhang J, Kapli P, Pavlidis P, Stamatakis A (2013) A general species delimitation method with applications to phylogenetic placements. Bioinformatics (Oxford, England) 29(22): 2869–2876. https://doi.org/10.1093/bioinformatics/btt499

Supplementary material 1

List of examined specimens

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Data type: docx

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Link: https://doi.org/10.3897/zse.101.157306.suppl1

Supplementary material 2

Downloaded sequences GenBank accession numbers

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Data type: xlsx

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Link: https://doi.org/10.3897/zse.101.157306.suppl2

Supplementary material 3

GenBank accession numbers of sequences generated in this study

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Data type: xlsx

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Supplementary material 4

bPTP support partitions

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Data type: pdf

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